

A Review of the Old World Genus *Fopius* Wharton (Hymenoptera: Braconidae: Opiinae), with Description of Two New Species Reared from Fruit-infesting Tephritidae (Diptera)

R. A. WHARTON

Department of Entomology, Texas A&M University, College Station, Texas 77843

Abstract.—Two new species of the Old World genus *Fopius* are described: *ceratitivorus* from Kenya and *schlingeri* from Queensland, Australia. Both species were reared from fruit-infesting Tephritidae; *ceratitivorus* from *Ceratitis* and *schlingeri* from *Bactrocera*. Details are provided on differentiation of the known species of *Fopius*, with discussion of their hosts, host specificity, and distribution. The parasitoids of fruit-infesting tephritids from Kenya are closely related to those from Madagascar.

The most recent comprehensive classification of the Opiinae is the three-volume monograph published by Fischer (1972, 1977, 1987). This collective work established a basis for more intense scrutiny of the Opiinae, resulting in several subsequent modifications and additions to the classification, including the description of the Old World genus *Fopius* (Wharton 1987, van Achterberg and Maetô 1990). The numerous name changes affecting opiine parasitoids of fruit-infesting Tephritidae were recently reviewed by Wharton (1997b), who also provided suggestions for delineation of species groups within the genus *Fopius*. Additional changes in nomenclature, some of these affecting opiine parasitoids of tephritids, were published by van Achterberg and Salvo (1997) and Quicke et al. (1997). Keys to most of the species of *Fopius* can be found in Wharton and Gilstrap (1983) and Fischer (1987), with both works treating the species under the generic name *Bios-teres*. Palacio et al. (1992) provide additional information on separation of males and immatures of two sympatric species.

All opiine braconids reared to date are koinobiont endoparasitoids of cyclorha-

phous Diptera, and all emerge from the puparium of their hosts. Hosts are known for one-third of the approximately 1500 described species, with most of these records pertaining to Agromyzidae and Tephritidae. All reared species of *Fopius* are parasitoids of Tephritidae. Summaries of the literature on hosts and biology of the opiine parasitoids of Tephritidae can be found in Fischer (1972, 1977, 1987), Clausen (1978), Wharton and Marsh (1978), Wharton and Gilstrap (1983), Gilstrap and Hart (1987), Wharton (1989, 1997a, b), Messing (1996), Sivinski (1996), and Sivinski et al. (1997).

The primary purpose of the work presented here is to facilitate on-going studies in biological control by providing names for two recently discovered, undescribed species. Both species are of interest with respect to tephritid biological control because of their potential for attacking eggs or early instars, and one of these is a native parasitoid of the Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann). The use of parasitic Hymenoptera for the biological control of tephritid pests has received considerable attention in recent years (Knippling 1992, Waterhouse 1993, Head-

rick and Goeden 1996, Purcell, 1998), and there are active programs currently underway in several countries.

MATERIALS AND METHODS

With the exception of *C. Granger's* type material from the Paris Museum and a single, swept specimen of *Fopius schlingeri*, n. sp., all material used in the descriptions of the new species was reared from fruit in association with various fruit-infesting Tephritidae. In some cases, parasitoids were reared from bulk fruit samples, with unconfirmed host associations. Most of the material, however, was reared from isolated puparia. In several of the rearings for *Fopius ceratitivorus*, n. sp., puparia were individually isolated prior to emergence. Though this procedure decreases the percent emergence (due primarily to desiccation and/or physical damage), it enables correct association of the wasp with the host from which it was reared.

Specimens of the newly described species have been deposited in the following institutions: University of Queensland, Brisbane (UQBA), Australian National Insect Collection, Canberra (ANIC), Texas A&M University, College Station (TAMU), Bernice P. Bishop Museum, Honolulu (BPBM), Hawaii Department of Agriculture, Honolulu (HDA), Queensland Department of Primary Industries, Indooroopilly (QDPI), Nationaal Natuurhistorisch Museum, Leiden (RMNH), The Natural History Museum, London (BMNH), National Museum of Kenya, Nairobi, International Centre of Insect Physiology and Ecology, Nairobi (ICIPE), and U.S. National Museum of Natural History, Washington, D. C. (USNM).

Descriptive terminology follows Wharton (1987, 1988, 1997b) and Sharkey and Wharton (1997), and is based largely on the works of Fischer (1972). A tabular summary is presented rather than a dichotomous key to facilitate assessment of relationships and point out gaps in our knowledge.

IDENTIFICATION, RELATIONSHIPS, HOSTS, AND DISTRIBUTION PATTERNS

The tephritid parasitoids in the genus *Fopius* are readily distinguished from other opiines by the possession of crenulate notauli extending posteriorly to the mesonotal midpit, an oblique ridge ventrolaterally on the propleuron, a short second submarginal cell ($3RSa \leq 2RS$), and a long ovipositor ($1.3\text{--}4.5 \times$ longer than mesosoma). Character states useful for identifying species with known tephritid host records are provided in Table 1, and the characters themselves are discussed below. Eight closely related species for which host records are lacking have also been included in the table. The table is deemed more informative than a dichotomous key because it provides preliminary data for phylogenetic analysis, which is beyond the scope and purpose of the present work, as well as providing supplemental characters for assistance in identification. More than half of the species in Table 1 (including several of the tephritid parasitoids) are known only from the type or the type plus a few other specimens. Additional collecting is essential before progress can be made in our understanding of these species. Individual species and species groups are treated further following discussion of the characters.

Character 1.—Striate sculpture on the second and third metasomal terga. 0 = striae absent; 1 = striae present on tergum 2 only; 2 = striae present on tergum 2 and at least base of tergum 3. For most species, assignment of either character state 0 or character state 1 is unambiguous. *Fopius deeralensis* (Fullaway), however, has weak striae on tergum 2, and the sculpture is not always readily visible (see diagnosis following description of *F. schlingeri*, n. sp.). *Fopius skinneri* (Fullaway), from the Philippines, is the only species in which striae are usually

Table 1. Matrix of coded character states for species in the genus *Fopius* (see text for character definition).

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
<i>denticulifer</i> (van Achterberg & Maetô)	0	0	0	2	5	1	0	0	3	1	0	4	4.1-4.6	0
<i>marangensis</i> (Fischer)	0	0	0	2	5	1	0	0	2b	1	?	4	1.7	?
<i>taivanicus</i> (Fischer)	0	0	0	2	5	1	0	0	2b	1	?	4	~3.0	0
<i>ruficornis</i> (Granger)	0	1	0	1,2	3	1	0	0	1	2	0	2	1.5	0
<i>rubrithorax</i> (Granger)	0	1	0	1	2	0	1	1	1	0	1	0	1.3	1
<i>bevisi</i> (Brues)	0	0	1	1	1	0	1	1	0	0	1	0	2.2-2.3	1
<i>desideratus</i> (Bridwell)	0	0	1	1	1	0	1	1	0	0,1	1	0	3.0-3.2	1
<i>niger</i> (Szépligeti)	0	0	1	1	1	0	1	1	0	1	0,1	0	2.6-2.7	1
<i>otototomianus</i> (Fullaway)	0	0	1	1	1	0	1	1	0	1	1	0	2.8	1
<i>rufotestaceus</i> (Granger)	0	0	1	1	1	0	1	1	1	0	0,1	0	2.0-2.3	1
<i>alternatae</i> (Tobias)	1	0	0	0	0	0	?	0	3	1	?	2	~1.25	?
<i>arisanus</i> (Sonan)	1	0	0	0	0	0	0	0	2	0,1	0	3	2.5-2.8	0
<i>carpomyiae</i> (Silvestri)	1	0	0	0	0	0	0	0	2a	0	1	2	1.5-1.7	0
<i>myoleiae</i> (Tobias)	1	0	0	0	0	0	?	0	3	1	?	2	~2.0	?
<i>persulcatus</i> (Silvestri)	1	0	0	0	0	?	0	0	2a	0	?	3	?	?
<i>skinneri</i> (Fullaway)	2	0	0	0	0	0	0	0	2b	1	0	3?	~2.65	0
<i>vandenboschi</i> (Fullaway)	1	0	0	0	0	0	0	0	2b	0,1	0	2	2.5-2.7	0
<i>ceratitivorus</i> n. sp.	0	0	0	0	5	0	0	0	0	0	0,1	2	1.7-1.9	0
<i>longicauda</i> (Granger)	0	0	0	0	0	0	0	0	1	0	0	2	2.6	1
<i>pyknothorax</i> (Fischer)	0	0	0?	?	?	?	?	0,1	0	1	?	?	?	?
<i>silvestrii</i> (Wharton)	0	0	0	0	0	0	0	0	0	1	0	2	2.5-2.6	0
<i>deeralensis</i> (Fullaway)	1	0	0	0,2	5	0	0	0	4	0	0	1	3	1
<i>schlingeri</i> n. sp.	0	0	0	0	5	0	0	0	4	0	0	3	2.3-2.5	1
<i>caudatus</i> (Szépligeti)	0	0	0	1	4	0	0	0,1	0	1	1	3	2	1

present on tergum 3, though the sculpturing on tergum 3 is usually not extensive.

Character 2.—Occipital carina. 0 = present laterally; 1 = completely absent. The occipital carina is absent mid-dorsally in *Fopius*, but present laterally in nearly all species. There is also some variation among species in the height of the occipital carina, as exemplified by the two species described below, and this variation may eventually prove useful in demonstrating character state transformations leading to complete loss of the occipital carina.

Character 3.—Setal pattern on the ovipositor sheath. 0 = two or more rows of densely spaced setae; 1 = setae sparse, at most with a row of long, moderately sparse setae basally and short, widely spaced setae apically. This coding is useful for segregating groups of species, but oversimplifies the complexity of the character states that may eventually be

useful for delineation of additional species. Setal rows are difficult to count, however, and many of the specimens examined were in such poor condition that it could not be determined if setae were sparsely arranged or merely broken off. Of the species coded 0 in Table 1, setal density was greatest in *F. denticulifer* (van Achterberg and Maetô) and least in *F. schlingeri*, n. sp. and *F. rubrithorax* (Granger).

Character 4.—Ventral margin of clypeus. 0 = thin, sharp, and evenly convex, without median projection; 1 = somewhat thickened medially, and slightly protruding, with labrum sometimes partially exposed; 2 = with median, ventrally-directed, tooth-like (i. e. pointed) projection (clypeus completely occludes labrum). Differences between states 0 and 1 may not be apparent without dissection to reveal the thickened margin. The tooth-like projection is very small in *deeralensis*, and the margin thinner than

in members of the *F. marangensis* (Fischer) species group, as reflected by its coding in Table 1.

Character 5.—Pattern of sculpture and setae on frons. 0 = densely setose and punctate, the punctures tending to coalesce to some degree, giving the appearance of transversely rugulose lines (Fig. 4), midline longitudinally rugose; 1 = transversely striate and impunctate over middle half of frons, with deep, widely spaced punctures laterally; 2 = laterally as in state 1, but largely unsculptured medially (at most with a few, irregular, very weak wrinkles), midline with sharp carina basally; 3 = smooth, impunctate, depressed along midline; 4 = broad, transverse band of deep punctures extending from ocelli to eye, otherwise smooth; 5 = densely setose and punctate, the punctures discrete, with no indication of rugosities as in state 0; for state 5, the punctures are very densely spaced in *marangensis*, *F. taiwanicus* (Fischer) and *denticulifer*, less so in *deeralensis* and *schlingeri*, and least in *ceratitivorius* (where they are virtually absent basal-laterally).

Character 6.—Postpectal carina. 0 = well developed; 1 = weak to absent.

Character 7.—Relative length of first two flagellomeres. 0 = first flagellomere about same length as second (ratio varying from 0.9–1.1); 1 = first flagellomere distinctly shorter than second (0.8 × length or less).

Character 8.—Shape of petiole. 0 = petiole length equal to or shorter than apical width, strongly widening apically; 1 = petiole appearing more parallel-sided, with length distinctly greater (at least 1.3 times) than apical width. The petiole of *F. caudatus* (Szépligeti) is somewhat intermediate, as reflected by its coding in Table 1. The petiole is not necessarily more parallel-sided in state 1 than in state 0 (width at apex may be twice width at base in both), but appears to

be so because the petiole is longer in state 1.

Character 9.—Geographic distribution. 0 = continental Africa; 1 = Madagascar; 2 = southern Asia (2a = India; 2b = southeast Asia, including Indonesia, Philippines, and Taiwan); 3 = Japan, eastern Russia; 4 = northeastern Australia. Distribution patterns given here do not reflect the successful introductions of *F. arisanus* (Sonan) and *F. vandenboschi* (Fullaway) to Hawaii and *arisanus* to Central America.

Character 10.—Color of mesosoma. 0 = largely pale (red, orange, yellow, or brownish-white); 1 = dark black to brown; 2 = pale with large black spots on mesoscutum and mesopleuron. Assessment of coloration is somewhat problematic due to postmortem changes, especially in shades of red, yellow, and orange. Also, there is almost a complete continuum in shades of red from pale through nearly black (*skinneri* is dark reddish-brown). Two of the species for which there is abundant material (e. g. *arisanus* and *vandenboschi*) are color-variable.

Character 11.—Dorsal carinae of petiole. 0 = dorsal carinae extending posteriorly beyond spiracle for at least a short distance as a distinctly elevated ridge; 1 = dorsal carinae not extending past spiracle as a distinctly elevated ridge. At least three species are variable in this feature, as reflected by the coding in Table 1.

Character 12.—Configuration of ovipositor tip. 0 = distinct double node dorsally; 1 = weak node or swelling dorsally; 2 = parallel-sided at apex, with little or no node; 3 = strongly tapered apically to a fine, smooth point, narrowest subapically; 4 = strongly tapered apically as in state 3, but with tip flattened dorsally-ventrally. States 1 and 2 merely represent different degrees of development of a transverse ridge near the tip of the ovipositor; and states 3 and 4 represent

conditions for which it is hypothesized here that nodes and/or transverse ridges have been lost. Detailed SEM work is still needed to elucidate these character states for many of the species.

Character 13.—Approximate ovipositor length. Values given are total ovipositor length divided by length of mesosoma. Accurate measurement of ovipositor length often requires dissection, which was not possible for some of the species.

Character 14.—Mesopleural setae. 0 = at least some setae present on mesopleuron dorsal to the speculum (the dorsal-posterior section of the mesopleuron); 1 = setae completely absent above speculum.

Table 1 has been arranged to facilitate identification of both species and species groups. Several of the species groups are quite distinctive and thus readily recognizable (Wharton 1997b), and these will be treated first in the following discussion. Since the focus of this paper is on parasitoids of fruit-infesting Tephritidae, *F. ruficornis* (Granger) and the *marangensis* species group are not further discussed because there are no host records and the species are readily identified using Table 1.

The *desideratus* species group of *Fopius* consists of *bevisi* (Brues), *desideratus* (Bridwell), *niger* (Szépligeti), *ottotomoanus* (Fullaway), and *rufotestaceus* (Granger). As noted by Wharton and Gilstrap (1983), the species of the *desideratus* group are very similar to one another. For example, *rufotestaceus* is virtually identical to *bevisi*, but has the mesosoma red rather than yellow or yellow-orange. Unfortunately, few specimens have been available for study of intraspecific variation in the color patterns currently used to differentiate the species of this group. There are published host records (summarized by Wharton and Gilstrap 1983) for all but *rufotestaceus*. Most of the specimens examined were reared from *Dacus* infesting Cucurbita-

ceae. Both *desideratus* and *ottotomoanus* have been recorded from undetermined species of *Dacus* in cucurbits (Bridwell 1919, Fullaway 1957), and *niger* was reared from *D. humeralis* Bezzi (Wharton and Gilstrap 1983). The few remaining published records (Bridwell 1919, Clausen et al. 1965) are from *Ceratitidis anonae* Graham on *Myrianthus arboreus* (specimens of *desideratus*) and *Trirhithrum queritum* Munro on *Strychnos usambarensis* (a specimen tentatively identified as *bevisi*). All members of this species group have large, subapical nodes on the ovipositor. Based on comparisons of ovipositor morphology with species of known biology in the related genus *Diachasmimorpha* Ashmead, it is suggested here that members of the *desideratus* group attack late instar larvae of their hosts. Members of this group are known from Cameroon, Kenya, Nigeria, Tanzania, South Africa, and Madagascar, and undoubtedly occur throughout sub-Saharan Africa. *Fopius rubrithorax* (Granger) is very similar to the other species mentioned here, despite the reduced sculpture on the frons and a slightly more setose ovipositor sheath; and I therefore place it as a basal member of this group. This placement assumes that both the reduced setal pattern on the ovipositor sheath and the pattern of sculpture on the frons of the five other species of the *desideratus* group are derived relative to the conditions in *rubrithorax*; this remains to be tested in a more rigorous fashion.

The *persulcatus* species group of *Fopius*, characterized largely by striate sculpture on the second metasomal tergum, consists of *alternatae* (Tobias), *arisanus* (Sonan), *carpomyiae* (Silvestri), *myolejae* (Tobias), *persulcatus* (Silvestri), *skinneri* (Fullaway), and *vandenboschi* (Fullaway). The species are very similar to one another, but differ primarily in coloration, length of ovipositor, and configuration of the ovipositor tip. Following their successful introduction to Hawaii during the biological control program against oriental fruit fly (Clausen et

al. 1965), *arisanus* and *vandenboschi* were intensively studied, and much is now known about their biology (with most of the early literature on *arisanus* published under the name *Opius oophilus* Fullaway). In their native range, centered around Malaysia and Indonesia, both are parasitoids of tephritids in the dacine genus *Bactrocera* Macquart. Unlike *skinneri*, neither is attracted to cucurbit-infesting flies. Other than the original host records little is known about the other species in this species group, including *skinneri*. Data on *persulcatus* (type material reared from *B. carayae* Kapoor) are particularly problematic because of widespread confusion regarding the identity of this species during the Hawaiian oriental fruit fly program, and the subsequent description of several subspecies (Fischer 1965). The other species (viz. *carpomyiae*, *myolejae*, and *alternatae*) have been reared, respectively, from trypetine tephritids in the genera *Carpomya* Costa, *Myoleja* Rondani, and *Rhagoletis* Loew. Based on the similarities in the shape of the ovipositor tip, all species in this species group preferentially attack either the egg or early instar larva of their host (though all eventually emerge from the puparium). This biology, however, has only been confirmed for *arisanus* (attacking eggs) and *vandenboschi* (attacking primarily first instars). The species of this group are known from Pakistan and India east through Indonesia and north through Taiwan, Japan, and far eastern Russia.

Wharton (1997b) delimited a *silvestrii* species group containing *longicauda* (Granger), *pyknothorax* (Fischer), and *silvestrii* (Wharton). One of the species described below, *ceratitivorus*, also belongs here. This group is currently defined largely by the absence of features that define the three species groups already mentioned: the clypeus lacks a median tooth on the ventral margin, the setae on the ovipositor sheath are not reduced, and the second metasomal tergum is unsculptured. Reduction of features on the dorsal

valve of the ovipositor suggests either a sister group relationship to the *persulcatus* species group or a parallel loss relative to the *desideratus* species group, but this hypothesis needs to be tested more rigorously. Both *silvestrii* and *ceratitivorus* have been reared from ceratitine tephritids infesting coffee, and *silvestrii* has also been reared from *Dacus bivittatus* (Bigot) infesting squash (Steck et al. 1986, Wharton 1987). Other members of this group have not been reared. Members of the *silvestrii* species group have much the same distribution pattern as those of the *desideratus* species group, and are differentiated from one another largely by color (*silvestrii* and *pyknothorax* are dark, *longicauda* and *ceratitivorus* are pale) and ovipositor length.

The remaining three species, *caudatus*, *deeralensis*, and *schlingeri*, do not readily cluster into distinctive species groups. Identification of *deeralensis* and *schlingeri* is discussed below under the diagnosis following the description of *schlingeri*; *caudatus* is readily separated from all other species of *Fopius* by the distinctive band of setae and punctures on the frons. Both *deeralensis* and *schlingeri* are from Queensland, where (as noted below under the description of *schlingeri* and in Clausen et al. 1965) they have been reared from various species of *Bactrocera* in a variety of host fruits. *Fopius caudatus* has thus far been reared exclusively from ceratitines (Steck et al. 1986). It is known from tropical regions of both eastern and western Africa, where it has been reared from coffee berries containing the ceratitines *Trirhithrum coffeae* Bezzi, *C. anonae* and *C. capitata* as well as from other fruits containing *anonae*. Specific host records for *caudatus* need confirmation, in part because of earlier confusion regarding its identity (Wharton 1987). This species resembles members of the *desideratus* species group in the morphology of the clypeus and petiole, but has a distinctly different ovipositor (strongly narrowed, suggesting oviposition in the host egg) as well as several fea-

tures unusual for members of the genus *Fopius* (Wharton 1997b).

A few generalizations can be made about hosts and distribution patterns, even though our current knowledge is somewhat limited. Rearing records from within their native ranges (Clausen et al. 1965, Steck et al. 1986) suggest that the 16 species for which we have host records are restricted to fruit-infesting tephritids, but that there are different levels of specificity. Some are currently known only from a single host, others (e. g. *caudatus* on ceratitines) have only been reared from a narrow group of hosts, and several have been reared from hosts in two or three different tribes. Most of the known hosts belong to the tribes Ceratitini and Dacini, both in the tephritid subfamily Dacinae (White and Elson-Harris 1992). Except where they have been introduced for biological control, members of the *persulcatus* group occur outside the range of fruit-infesting Ceratitini, and several of them have been reared from Trypetini in the tephritid subfamily Trypetinae. Where introduced outside their native range for biological control, *arisanus* and *vandenboschi* have been able to attack other fruit-infesting tephritids (Clausen et al. 1965, Wharton et al. 1981). Yet, while some of the species of *Diachasmimorpha* Viereck introduced to Hawaii to control fruit-infesting Tephritidae occasionally attack gall-making (but not flower-infesting) Tephritidae, *arisanus* and *vandenboschi* do not (Duan et al. 1996).

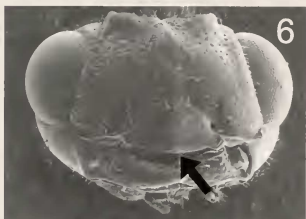
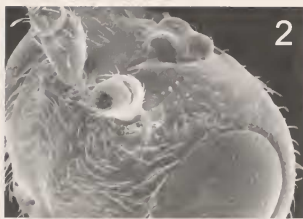
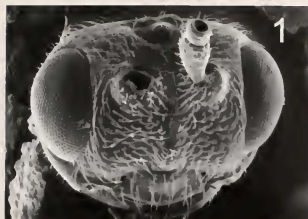
The genus *Fopius* provides evidence for a close relationship between the fauna of Madagascar and that of adjacent regions of continental Africa (as do its host tephritids). Although a few of the Madagascar elements (notably *rubrithorax* and especially *ruficornis*) are unique in several respects, both *rufotestaceus* and *longicauda* have their closest known relatives (*bevisi* and *ceratitivorus* respectively) on the adjacent mainland.

DESCRIPTIONS

Fopius ceratitivorus Wharton, new species

(Figs. 1, 2, 7, 8, 10, 11, 13–15, 21)

Female.—**Head**: 1.55–1.75 ($m=1.65\pm.07$) times broader than long; 1.25–1.35 times broader than mesoscutum; face distinctly punctate throughout, pattern variable but spacing between most punctures about equal to diameter of punctures; setae short, somewhat decumbent; midridge low, polished, more prominent dorsally, extending between antennal bases (toruli) as a low, flat ridge; distance between toruli greater than distance from torulus to eye; frons longitudinally rugulose along midline, highly polished and weakly depressed basally on either side of rugulose midline, deeply punctate elsewhere, the patch of punctures on each side anteriorad ocelli usually more densely spaced, occasionally with punctures coalescent, ocellar triangle almost completely margined by a crenulate sulcus. Occipital carina in lateral view extending dorsally from base of mandible to a point just below top of eye. Clypeus in profile slightly bulging dorsomedially; ventral margin of clypeus thin and evenly convex, not thickened medially; setae on clypeus very sparse, at least twice length of those in middle of face, weakly directed ventrally; clypeus completely concealing labrum when mandibles closed. Eye (at 50 $\times$) apparently bare, large, 2.85–3.8 ($m=3.2\pm0.3$) times longer temple; temples very weakly receding in dorsal view; width of head at temples slightly less than width at eyes. Antenna 31–37 segmented; roughly 3.0–3.1 times longer than mesosoma; first flagellomere 0.9–0.95 times length of second. Maxillary palps longer than height of head. **Mesosoma**: 1.25–1.35 ($m=1.3\pm0.05$) times longer than high, 1.55–1.7 ($m=1.65\pm0.05$) times longer than broad. Median lobe of mesoscutum with 2 parallel, rugosopunctate, longitudinal grooves extending more than half length of median lobe, median lobe otherwise setose, with



Figs. 1–6. Heads of *Fopius* spp.: 1 and 2, *ceratitivorus* frons and face; 3, *schlingeri* face and clypeus; 4, *arisanus* frons; 5, *schlingeri* face and clypeus; 6, *deeralensis* face and clypeus (most setae broken), arrow = median projection on ventral margin of clypeus.

scattered, deep punctures; lateral lobes bare and impunctate medially, with numerous, relatively long, inwardly directed setae around margins; notauli broadening posteriorly, distinctly crenulate throughout, with pits usually becoming elongate posteromedially where the ridges between the pits form a small strigose area; space

between strigose area and scutellar sulcus with scattered, deep punctures, postero-medial area either broadly and very shallowly depressed or with a shallow, more discrete midpit. Scutellar sulcus broader medially than laterally, the posterior margin with a distinct median excavation; number of longitudinal ridges in sulcus

variable. Metanotum with relatively low median ridge. Propodeum finely, densely rugose, the sculpture without obvious pattern; elevated median longitudinal carina usually distinct only on anterior 0.25–0.35; propodeum laterally not separated from metapleuron by a well-defined pleural carina, the demarcation represented only by the transition to the weakly sculptured dorsal portion of the metapleuron. Sternaulus broad, deep, crenulate throughout, extending posteriorly roughly 0.7 times distance from anterior margin of mesopleuron to mid coxa; crenulate sculpture extending dorsally along anterior margin of mesopleuron through subalar depression; posterior margin crenulate ventrad speculum, but with unsculptured sulcus dorsally; mesopleural disc setose throughout; postpectal carina present, but variously developed. **Wing:** Stigma 2.7–2.9 ($m=2.85\pm0.1$) times longer than wide, with *r* arising slightly distad its midpoint; 2RS weakly sinuate, 1.2–1.45 ($m=1.3\pm0.05$) times longer than 3RSa; 3RSa 1.55–2.5 ($m=2.1\pm0.3$) times longer than *r*; 3RSb ending slightly but distinctly anteriorad wing tip; (RS+M)a sinuate; (RS+M)b present, m-cu nearly always arising distinctly basad 2RS; 1cu-a inclivous, usually postfurcal relative to 1M but varying from interstitial to postfurcal by 0.4 times its length. Hind wing m-cu reclivous, straight or very weakly recurved near wing margin, extending to wing margin or nearly so as well-developed, deeply impressed crease, usually weakly pigmented anteriorly. **Metasoma:** Petiole 0.95–1.05 ($m=1.0\pm0.05$) times longer than apical width, apex 1.80–2.15 ($m=1.95\pm0.1$) times wider than base; densely and finely striate; dorsal carinae well-developed over basal two-thirds, weaker posteriorly but distinct to posterior margin, carinae very weakly converging, with distance between carinae at posterior margin roughly equal to distance to lateral margin; dorsope present but not extending basally as a deep pit. Metasoma unsculptured beyond petiole. Hypopygium strongly narrowed and

pointed posteriorly but short, not greatly attenuate. Ovipositor tip weakly narrowed apically, without distinct dorsal node or carina but with weak ventral serrations; 1.65–1.95 ($m=1.8\pm0.1$) times longer than mesosoma; ovipositor sheath densely setose with multiple rows of at least 30 setae each, the number of rows difficult to distinguish because of density of setae; sheath 1.35–1.55 ($m=1.45\pm0.05$) times longer than mesosoma. **Color:** Pale, yellow to orange, the exact hue dependent largely on manner of preservation; ovipositor sheath, veins, and stigma brown; antenna brown, with scape, pedicel, and basal flagellomeres usually yellow to orange medially. Wings hyaline.

Male.—As in female except eye 2.9 ± 0.25 times longer than temple; antenna 30–35 segmented; petiole narrowed at apex, 1.1–1.25 ($m=1.15\pm0.05$) times longer than apical width, apex 1.6–1.95 ($m=1.75\pm0.1$) times wider than base; dorsope less distinct. **Length:** 2.0–3.4 (♀) and 1.85–2.9 (♂) mm.

Hosts.—This species has been reared from isolated puparia of fruit-infesting Tephritidae attacking coffee in central Kenya. It has also been reared from bulk samples of coffee. The tephritids from these samples, in order of abundance, were *Ceratitidis capitata*, *C. rosa* Karsch, and *Trirhithrum coffeae*. All are members of the tribe Ceratitini, subtribe Ceratitina.

Material examined.—Holotype female, "Kenya: Ruiru C. R. F. 17.IX.1996 ex: tephritid on coffee berries Ref. No. CB03" Deposited in Kenya National Museum, Nairobi. Paratypes (BMNH, BPBM, RMNH, HDA, ICIPE, TAMU, USNM): 5♀, 7♂, "Kenya: Nairobi 20.v.1997 ex: *Ceratitidis capitata*, coffee M. Ramadan & R. Messing"; 33♀, 25♀, "Kenya E. Province, Mbeere Distr Mbeti south Furima 30.iv.97 ICIPE Fruitfly Project ex Fruitfly on Coffee berries"; 1♀, 1♂, "Kenya: Ruiru 15mi NNE Nairobi 10.iv.1995 ex: coffee No. CB05 ICIPE Collections"; 1♀, "Kenya: Western Prov. Koru iv.1995 ex. *Coffea canephora* CAB Collections" and, 1♂



Figs. 7–10. *Fopius* spp.: 7, *ceratitivorus* head, arrows = top of occipital carina and mid-dorsal elevation of clypeus; 8 and 10, *ceratitivorus* dorsal view of mesosoma; 9, *schlingeri* dorsal view of mesosoma.

"Kenya: E. Province Mbeere District Rurima Farm 0°38'29"S, 37°29'49"E 3.x.1997 ex tephritid in coffee Wharton, Kimani, Overholt." This species is known only from central Kenya.

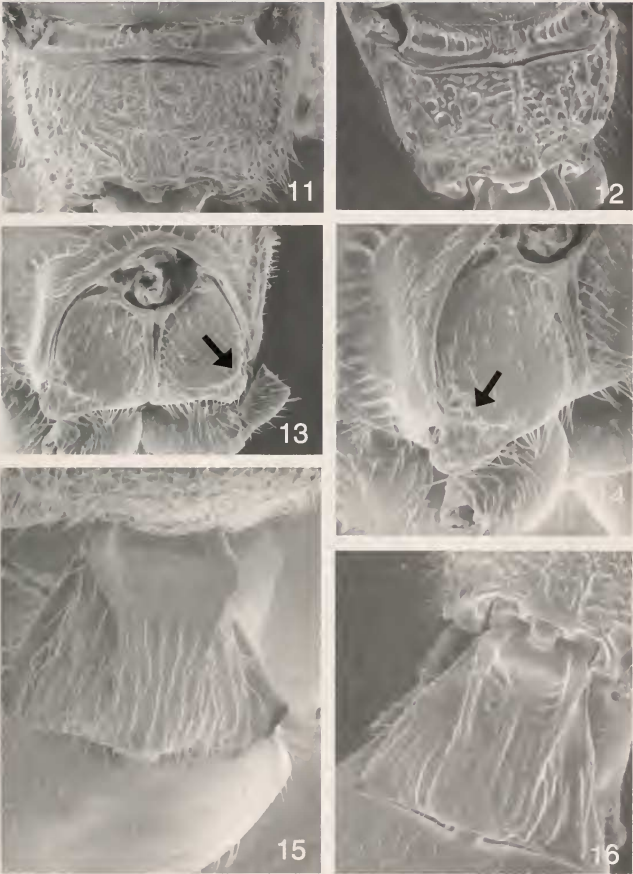
Diagnosis.—This species closely resembles *longicauda*, known only from Madagascar. The two species are similarly colored, have a densely punctate frons, densely setose ovipositor sheath, and identical configuration of the clypeus. *Fopius ceratitivorius* differs from *longicauda* primarily in the possession of a shorter ovipositor (sheaths at least 2 times longer than mesosoma in *longicauda*). The median lobe of the mesoscutum and the junction of the notauli (Fig. 10) are also more heavily sculptured in *ceratitivorius* than in *longicauda*, and hind wing m-cu is straighter. Both *ceratitivorius* and *longicauda* differ from other Old World species of *Fopius* either in coloration, sculpture of the frons, length of ovipositor, and/or shape of the clypeus and its relative degree of concealment of the labrum. From other orange opiines reared from tephritids in coffee in Kenya, *ceratitivorius* may be readily distinguished by the short second submarginal cell with fore wing m-cu distinctly separated from 2RS (Fig. 21) and by the completely sculptured notauli.

Discussion.—I place *ceratitivorius* in the *silvestrii* species group of *Fopius* (Wharton 1997b). The ovipositor tip of *ceratitivorius*, though narrowed, does not have exactly the same morphology as found in *arisanus* and *schlingeri* n. sp. Thus, females probably do not oviposit in host eggs, but based on the shape of the ovipositor tip, they may attack early instars. The same may be true of *longicauda*, the holotype of which appears to have a similar ovipositor.

A weak negative correlation was observed between body length and relative length of the ovipositor, but the sample size ($N=10$) was too small to confirm this apparent trend.

***Fopius schlingeri* Wharton, new species**
(Figs. 3, 5, 9, 12, 16, 18–20)

Female.—**Head:** $1.55\text{--}1.65$ ($m=1.6\pm.05$) times broader than long; $1.3\text{--}1.4$ ($m=1.35\pm.05$) times broader than mesoscutum; face distinctly punctate throughout, pattern variable but spacing between most punctures distinctly greater than diameter of punctures; setae short, somewhat decumbent; midridge low, polished, narrower dorsally, extending between toruli; distance between toruli varying from slightly to distinctly greater than distance from torulus to eye; frons with polished, weakly elevated, crenulately margined, triangular projection extending from median ocellus at least half distance to torulus; frons otherwise punctate, the punctures anteriorad ocellar field dense, with spacing between punctures about equal to diameter of punctures; ocellar triangle margined at least in part by an impressed line. Occipital carina in lateral view extending dorsally from base of mandible to about middle of eye. Clypeus in profile weakly to distinctly bulging dorsomedially; ventral margin of clypeus thin and weakly but evenly convex, not thickened medially nor with median projection; setae on clypeus sparse, about twice length of those on face, weakly directed ventrally; ventral margin of clypeus not sufficiently convex to completely conceal labrum when mandibles closed. Eye usually with 1–4 minute setae visible in dorsal view, very large, $5.3\text{--}7.5$ ($m=6.45\pm.075$) times longer than temple; temples weakly receding in dorsal view; width of head at temples about 0.9 times width at eyes. Antenna 41–47 segmented; roughly 3.5 times longer than mesosoma; first flagellomere equal in length to second. Length of maxillary palps equal to height of head. **Mesosoma:** $1.25\text{--}1.35$ ($m=1.3$) times longer than high, $1.75\text{--}1.80$ times longer than broad. Median lobe of mesoscutum with 2 parallel, unsculptured, longitudinal grooves extending more than half length



Figs. 11–16. *Fopius* spp.: 11, *ceratitivorus* propodeum; 12, *schlingeri* propodeum; 13 and 14, *ceratitivorus* propleuron, arrow = oblique carina; 15, *ceratitivorus* petiole; 16, *schlingeri* petiole.



Figs. 17 and 18. Ovipositors of *Fopius* spp: 17, *deeralensis*; 18, *schlingeri*.

of median lobe, median lobe otherwise setose with numerous, very fine, widely spaced punctures; lateral lobes with numerous, relatively long setae around margins and more sparsely scattered setae medially; notauli distinctly crenulate throughout, meeting posteriorly in a clearly defined midpit that often extends narrowly to posterior margin. Scutellar sulcus parallel sided or nearly so, usually with 3 well-developed longitudinal carinae plus several additional weaker ones. Metanotum with distinctly elevated median flange posteriorly. Propodeum densely rugose, the sculpture largely without obvious pattern though elevated median longitudinal carina distinct on anterior 0.25, and posterior 0.25 often with remnants of the parallel ridges from a median areola; propodeum laterally not separated from metapleuron by a well-defined pleural ca-

rina, the demarcation represented only by the transition to the weakly sculptured dorsal portion of the metapleuron. Sternaulus broad, deep, crenulate throughout, extending posteriorly roughly 0.7 times the distance from anterior margin of mesopleuron to mid coxa; crenulate sculpture extending dorsally along anterior margin of mesopleuron throughout subalar depression; posterior margin crenulate ventrad speculum, with unsculptured sulcus dorsally; mesopleural disc setose; postpectal carina well developed medially. Wing: Stigma 2.6–3.0 ($m=2.8\pm0.15$) times longer than wide, with r arising slightly distad its midpoint; 2RS nearly as sinuate as (RS+M)a, 1.15–1.3 ($m=1.25\pm0.05$) times longer than 3RSa; 3RSa 1.7–2.25 ($m=1.9\pm0.2$) times longer than r ; 3RSb ending nearly at wing tip; (RS+M)a sinuate; (RS+M)b present and fairly long,

roughly 0.25 times length of m-cu; 1cu-a inclivous, usually slightly postfurcal relative to 1M but varying from nearly interstitial to postfurcal by 0.5 times its length. Hind wing m-cu strongly reclivous, distinctly recurved near wing margin, extending to wing margin or nearly so as a deeply impressed, completely pigmented crease. **Metasoma:** Length of petiole 0.85–0.95 ($m=0.9\pm0.05$) times width at apex; apex 2.3–2.5 ($m=2.4\pm0.1$) times wider than base; moderately and somewhat irregularly striate posteriorly; dorsal carinae well-developed over basal two-thirds, weaker posteriorly, often indistinct at posterior margin, parallel to very weakly converging posteriorly; dorsope weakly developed. Metasoma unsculptured beyond petiole. Hypopygium strongly narrowed and distinctly pointed at extreme posterior end, but short, not greatly attenuate, length along midline about 0.55 times width at base. Ovipositor tip strongly narrowed subapically, without dorsal node or carina, ventral serrations indistinct to absent; 2.3–2.55 ($m=2.4\pm0.1$) times longer than mesosoma; ovipositor sheath moderately setose with 3 rows of setae, two of which have 30–35 setae per row with the third row more sparsely setose, distinct tuft of longer setae at apex, sheath 2.0–2.25 ($m=2.09\pm0.1$) times longer than mesosoma. **Color:** Orange; propleuron and propodeum often paler, at least in part, sometimes nearly white; ovipositor sheath, hind tarsi, flagellum, and sometimes pedicel dorsally brown to light brown; base of arolium dark brown. Wings weakly to distinctly infumate: more noticeably infumate in larger specimens.

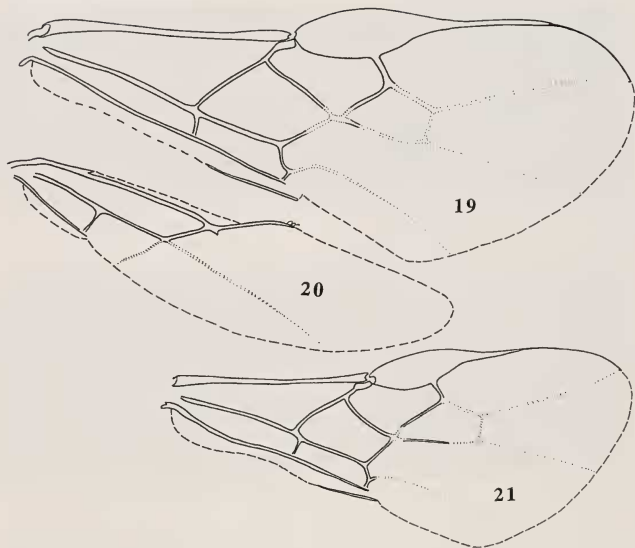
Male.—As in female except eye distinctly smaller, 4.4–5.85 ($m=5.15\pm0.5$) times longer than temple; petiole narrower at apex with length equal to apical width and apex 1.95–2.25 ($m=2.15$) times wider than at base. **Length:** 3.05–4.9 mm.

Hosts.—This species has been reared from guava (Myrtaceae) infested with *Bactrocera tryoni* (Froggatt), *Rauwenhoffia lei-*

chardtii (Annonaceae) infested with *B. halfordiae* (Tryon) and *B. neohumeralis* (Hardy), *Syzygium bamagense* (Myrtaceae) infested with *B. rufofuscula* (Drew and Hancock), and *Fagraea cambagei* (Loganiaceae) infested with *B. peninsularis* (Drew and Hardy). It thus appears to be able to attack several species of *Bactrocera* (Tribe Dacini) developing in the fruit of at least three plant families.

Material examined.—Holotype female, "Australia: QLD Mt. Glorious 26.i.1994 G. Quimio MG9413 ex: Rauwenhoffia lei-chardtii fruit containing Bactrocera halfordiae and B. neohumeralis" Deposited in ANIC. Paratypes (ANIC, BMNH, QDPI, TAMU, UQBA, USNM): 17♀, 17♂, same data as holotype; 2♀, 2♂, "Nambour Qld 24.iv.95 Guava G. Quimio"; 2♀, 1♂, same data except 29.v.95; 1♀, "Australia: QLD Wongabel 6 km S Atherton 1-28-1990 R. Wharton; 1♀, "Malanda NQ 22.xi.1987 M. Elson-Harris Ex Dacus rufofuscus 249"; 2♀, "Sydney, N.S.W., 28-6.1954 G. J. Snowball" one of these with an additional label "37/54" and the other "51/54". Additional material (not paratypes): 11♀, 3♂, Australia, North Queensland, Balinda, 10.vi.1993 from fruits of *Fagraea cambagei* infested with *Bactrocera peninsularis*. This species is known only from the eastern coast of Australia.

Diagnosis.—As with *ceratitivorius*, *schlingeri* also closely resembles the Madagascar species *longicauda*. The latter has a smaller eye (slightly less than 4 times longer than temple), somewhat more densely setose ovipositor sheath, a smaller gap between clypeus and mandibles when mandibles closed, and the distal portion of the ovipositor is parallel-sided rather than subapically narrowed relative to *schlingeri*. Of the species known from Queensland, *schlingeri* most closely resembles *deeralensis*. The latter has the ventral margin of the clypeus distinctly pointed midventrally (Fig. 6, with mid-ventral projection more distinct when head rotated forward), a distinct subapical ridge on the ovipositor



Figs. 19–21. Wings of *Fopius* spp.: 19 and 20, *schlingeri* fore and hind wing; 21, *ceratitivorius* fore wing.

(Fig. 17), and the second metasomal tergum is usually weakly striate, at least basally.

Discussion.—Wharton (1997b) observed that the hypopygium is strongly attenuate in many of the parasitoids of fruit-infesting Tephritidae. He also noted in his re-description of *Fopius* that the hypopygium varies from weakly to strongly produced posteromedially. Though distinctly narrowed and projecting posteriorly in both *ceratitivorius* and *schlingeri*, the hypopygium is much less strongly produced than it is in members of the *Fopius marangensis* species group or in other fruit-infesting tephritid parasitoids such as the members of the *Diachasmimorpha longicaudata* (Ashmead) species group or the species of *Psyt-*

talia. Fischer (1987) includes species with a partially visible labrum in *Diachasma* Foerster. Wharton (1997b) briefly discussed variation in this character, noting that some of the "variation" can be attributed to angle of view or the degree to which the mandibles are closed on any given specimen (compare Figs. 3 and 5). Nevertheless, there are slight differences among species of *Fopius* in the exposure of the labrum, and *schlingeri* provides a good example of a species with a partially exposed labrum (in contrast to the completely concealed labrum of *ceratitivorius*). The ovipositor in *schlingeri* (Fig. 18) is virtually identical in form to that of *arisanus*, strongly suggesting a biology similar to the latter in which the

parasitoid oviposits into the egg of its host. Field observations kindly supplied by Greg Quimio of the University of Queensland support this.

ACKNOWLEDGMENTS

I am especially grateful to the following collaborators for providing reared material for this study: M. Elson-Harris, F. Gilstrap, S. Kimani, C. Lopez-Vaamonde, S. Lux, R. Messing, W. Overholt, G. Quimio, M. Ramadan, G. Steck, and T. Wong. I also thank M. Trostle and S. Kimani for assistance in isolating puparia from which *Fopius ceratitivorus* were reared. Additionally, the following people kindly made material available for examination, without which the comparative aspects of this work would have been impossible: Greg Daniels and Gimme Walter (UQBA, Brisbane), Ian Naumann (ANIC, Canberra), David Wahl (American Entomological Institute, Gainesville), Valter Raineri (Museo Civico di Storia Naturale "Giacomo Doria," Genoa), Gordon Nishida, Keith Arakawa, and David Preston (BFBM, Honolulu), Dick Drew and all the members of his research group (formerly at QDPL, Indooroopilly), Kaoru Maetô (Shikoku Research Centre, Kochi), Tom Huddleston (formerly at BMNH, London), Ermenegildo Tremblay (Università di Napoli, Naples), Claire Villemant (Muséum National d'Histoire Naturelle, Paris), Sergey Belokobylskij (Zoological Institute, St. Petersburg), Zafar Qureshi, Atomic Energy Research Centre, Tandoo Jam, and Paul Marsh and David Smith (Systematic Entomology Laboratory, USDA, Washington, D. C.). This work was funded in part by USDA-CSREES Special Grant No. 96-34135, Tropical and Subtropical Agriculture Research (to R. Messing), USDA/NRI, and the National Science Foundation (DEB9712543), with additional travel support in Australia provided by R. A. I. Drew and A. Austin. Support of the Texas Agriculture Experiment Station, the International Centre of Insect Physiology and Ecology, and The Electron Microscopy Center of Texas A&M University is also gratefully acknowledged. Finally, I am indebted to Nando Bin for assistance in obtaining specimens, and Imelda Mercado, Ken Wilks, and Randy Scott for illustrations.

LITERATURE CITED

- Bridwell, J. C. 1919. Descriptions of new species of hymenopterous parasites of muscoid Diptera with notes on their habits. *Proceedings of the Hawaiian Entomological Society* 4: 166-179.
- Clausen, C. P. 1978. Tephritidae (Trypetidae, Trupaeidae), pp. 320-335. In: C. P. Clausen (ed.). Introduced parasites and predators of arthropod pests and weeds: a world review. *United States Department of Agriculture Agricultural Handbook* No. 480.
- Clausen, C. P., D. W. Clancy and Q. C. Chock. 1965. Biological control of the Oriental fruit fly (*Dacus dorsalis* Hendel) and other fruit flies in Hawaii. *United States Department of Agriculture Technical Bulletin* 1322: 1-103.
- Duan, J. J., M. F. Purcell and R. H. Messing. 1996. Parasitoids of non-target tephritid flies in Hawaii: implications for biological control of fruit fly pests. *Entomophaga* 41: 245-256.
- Fischer, M. (1963) 1965. Die orientalischen und australischen Arten der Gattung *Opius* Wesm. *Acta Entomologica Musei Nationalis Pragae* 35: 197-242.
- Fischer, M. 1972. Hymenoptera: Braconidae (Opiinae I). *Das Tierreich* 91: 1-620.
- Fischer, M. 1977. Hymenoptera: Braconidae (Opiinae II-Amerika). *Das Tierreich* 97: 1-1001.
- Fischer, M. 1987. Hymenoptera: Opiinae III—äthiopische, orientalische, australische und ozeanische Region. *Das Tierreich* 105: 1-734.
- Fullaway, D. T. 1957. A new reared *Opius* from Africa (Hymenoptera, Braconidae). *Proceedings of the Entomological Society of Washington* 59: 98-99.
- Gilstrap, F. E. and W. G. Hart. 1987. Biological control of the Mediterranean fruit fly in the United States and Central America. *United States Department of Agriculture ARS-56*: 1-64.
- Headrick, D. H. and R. D. Goeden. 1996. Issues concerning the eradication or establishment and biological control of the Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann) (Diptera, Tephritidae), in California. *Biological Control* 6: 412-421.
- Knipling, E. F. 1992. Principles of insect parasitism analyzed from new perspectives: practical implications for regulating insect populations by biological means. *United States Department of Agriculture Handbook* 693: 1-337.
- Messing, R. M. 1996. Status and needs of biological control research for tephritid flies, pp. 365-367. In: McPherson, B. A. and G. J. Steck (eds.). *Fruit Fly Pests—A world assessment of their biology and management*. St. Lucie Press, Delray Beach, Florida.
- Palacio, I. P., R. Ibrahim and A. G. Ibrahim. 1992. Identification of immatures and male adults of the opiine parasitoids (*Biosteres* spp.) of the Oriental fruit fly, *Bactrocera dorsalis* (Hendel). *The Philippines Entomologist* 8: 1124-1146.
- Purcell, M. 1998. Contributions of biological control to integrated pest management of tephritid fruit flies in the tropics and subtropics. *Integrated Pest Management Reviews* 3: 1-21.
- Quicke, D. L. J., K. van Achterberg and H. C. J. Godfray. 1997. Comparative morphology of the venom gland and reservoir in opiine and alysiine braconid wasps (Insecta, Hymenoptera, Braconidae). *Zoologica Scripta* 26: 23-50.
- Sharkey, M. J. and R. A. Wharton. 1997. Morphology and Terminology, pp. 19-37. In: Wharton, R. A.,

- P. M. Marsh, and M. J. Sharkey (eds.). *Manual of the New World Genera of the Family Braconidae (Hymenoptera)*. Special Publication of the International Society of Hymenopterists 1.
- Sivinski, J. 1996. The past and present of biological control of fruit flies, pp. 369–375. In: McPherson, B. A. and G. J. Steck (eds.) *Fruit Fly Pests—A world assessment of their biology and management*. St. Lucie Press, Delray Beach, Florida.
- Sivinski, J., M. Aluja and M. Lopez. 1997. Spatial and temporal distributions of parasitoids of Mexican *Anastrepha* species (Diptera: Tephritidae) within the canopies of fruit trees. *Annals of the Entomological Society of America* 90: 604–618.
- Steck, G. J., F. E. Gilstrap, R. A. Wharton and W. G. Hart. 1986. Braconid parasitoids of Tephritidae (Diptera) infesting coffee and other fruits in west-central Africa. *Entomophaga* 31: 59–67.
- Tobias, V. I. (1977) 1978. The genus *Opius* Wesm. (Hymenoptera, Braconidae) as parasites of fruit flies (Diptera, Tephritidae). *Entomological Review* 56: 132–139.
- Van Achterberg, C. and K. Maetô. 1990. Two new aberrant species of Braconidae (Hymenoptera) from Japan. *Zoologische Mededelingen Leiden* 64: 59–70.
- Van Achterberg, C. and A. Salvo. 1997. Reared Opiinae (Hymenoptera: Braconidae) from Argentina. *Zoologische Mededelingen Leiden* 71: 189–214.
- Waterhouse, D. F. 1993. *Biological Control: Pacific Prospects—Supplement 2*. Australian Centre for International Agricultural Research, Canberra. 138 pp.
- Wharton, R. A. 1987. Changes in nomenclature and classification of some opiine Braconidae (Hymenoptera). *Proceedings of the Entomological Society of Washington* 89: 61–73.
- Wharton, R. A. 1988. Classification of the braconid subfamily Opiinae (Hymenoptera). *The Canadian Entomologist* 121: 333–360.
- Wharton, R. A. 1989. Classical Biological Control of Fruit-infesting Tephritidae, pp. 303–313. In: Robinson, A. S. and G. Hooper (eds.). *Fruit Flies, Their Biology, Natural Enemies and Control*. Elsevier Science Publishers B.V., Amsterdam.
- Wharton, R. A. 1997a. Subfamily Opiinae, pp. 378–395. In: Wharton, R. A., P. M. Marsh, and M. J. Sharkey (eds.). *Manual of the New World Genera of the Family Braconidae (Hymenoptera)*. Special Publication of the International Society of Hymenopterists 1.
- Wharton, R. A. 1997b. Generic relationships of opiine Braconidae (Hymenoptera) parasitic on fruit-infesting Tephritidae (Diptera). *Contributions of the American Entomological Institute* 30: 1–53.
- Wharton, R. A. and F. E. Gilstrap. 1983. Key to and status of opiine braconid (Hymenoptera) parasitoids used in biological control of *Ceratitis* and *Dacus* s. l. (Diptera: Tephritidae). *Annals of the Entomological Society of America* 76: 721–742.
- Wharton, R. A., F. E. Gilstrap, R. H. Rhode, M. Fischel-M. and W. G. Hart. 1981. Hymenopterous egg-pupal and larval-pupal parasitoids of *Ceratitis capitata* and *Anastrepha* spp. in Costa Rica. *Entomophaga* 26: 285–290.
- Wharton, R. A. and P. M. Marsh. 1978. New World Opiinae (Hymenoptera: Braconidae) parasitic on Tephritidae (Diptera). *Journal of the Washington Academy of Sciences* 68: 147–167.
- White, I. M. and M. M. Elson-Harris. 1992. *Fruit Flies of Economic Significance: Their Identification and Bionomics*. CAB International, London and ACIAR, Canberra. 601 pp.